

THE
BOTANICAL GAZETTE

AUGUST 1919

A SPORANGIOPHORIC LEPIDOPHYTE FROM THE
CARBONIFEROUS

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(WITH PLATES IX-XI)

The plant impressions which form the subject of this paper have in part been known for several decades, but the discovery by the writer of the key to their important and very interesting nature came as a pleasant incident in monographic studies of the very large and varied flora of the Maryland Carboniferous, and it is believed that the testimony which they contribute to a discussion of the problem of the phylogeny of the vascular cryptogams will justify the publication of this paper in advance of the large systematic work upon which the writer is engaged.

These plant impressions were long regarded as the sporophylls of *Lepidostrobus* (*Lepidophyllum*), and latterly (16) certain of them were thought to be the microsporophylls of some yet unknown type of *Lepidostrobus* or *Lepidocarpon* whose sporangia by their complicated form, not then understood, differed from those of the known species of *Lepidophyllum*, but the writer will show that they differ so fundamentally from all known cryptogamic sporophylls that it will be necessary to establish for their reception a new genus. The most distinctive feature of this group is a large lamellar sporangiophore developed in the radial plane of the strobilus from the superior (ventral) face of the sporophyll pedicel, bearing two large elongate sporangia, one upon each side, pannier-like; and it is this character which has suggested the name *Cantheliophorus*,

from *καρθήλια*, the classic term for packsaddles with baskets or panniers.

NATHORST in 1914 (16) had a vague suspicion concerning the nature of one of the species now included within the genus under discussion, *Lepidophyllum mirabile* Nath. from the Lower Carboniferous of Spitzbergen, and this he expressed when he ventured two hypotheses: (1) that we may be dealing with a sporangium in which longitudinal sterile plates such as we observe in certain sporangia of *Lepidostrobus* were developed to a point where they divided it into distinct and separate loculi, 2 loculi where the plate is simple and 3 where it forks, somewhat after the manner of the sterile plate figured by WILLIAMSON (37) (fig. 41); or (2) that this structure may consist of 2 concrescent sporophylls of which the lower bearing the blade is sterile, while the upper bearing 2 sporangia is fertile. While the nature of the material was such that its real character was not apparent, NATHORST's very suggestive speculation concerning it prepares us somewhat for the discovery that the Carboniferous Lepidophytes are not the homogeneous stereotyped group they were long supposed to be.

The number of the sporangia subtended by each sporangiferous bract or sporophyll and the manner of their attachment have figured so largely in recent discussion of the phylogeny of the vascular cryptogams that we believe that some of this evidence should be re-examined in the light of the discovery of a truly sporangiophoric Lepidophyte in the Carboniferous, and after a comprehensive discussion of the characters of this new genus as a whole we shall devote some space to phyletic considerations.

Material

Lepidophyllum linearifolium Lesq., the first species of this group to be recognized, was described in 1880 by LESQUEREUX (13) from 5 good representative specimens from Pittston, Pennsylvania, and a fragmentary one, the nature of which is much in doubt, from Cannelton, Pennsylvania, all in the Lacoe Collection now at the United States National Museum,¹ and it is to be deplored that the

¹Where, as in this case, there is slight discrepancy between the statement of occurrence on the labels pasted to the specimens and that made by LESQUEREUX in his *Coal Flora*, I shall record the former.

latter, consisting of nothing but a nondescript blade with the fragment of a pedicel attached, should have been selected for figuring. I am able to figure here the cotype from Pittston, together with several specimens from a large collection made by the writer in the Youghiogheny Gorge below Swallow Falls, Garrett County, Maryland, one of them showing a somewhat impoverished sporangium (partly cut away) still attached to the sporangiophore. Here, as in each of the other already recognized species of this group, the sporangiophore has been mistaken for a flattened sporangium. The second species to be recognized was noted very briefly by LESQUEREUX in 1880 in concluding remarks on *L. linearifolium*, and it was not until 1884 that there appeared in the *Coal Flora* (3:785) a brief specific description under the name *Lepidophyllum cultriforme*. Two "forms" were there recognized but were not separated even varietally. One from Cannelton is represented on *pl. 108, fig. 2*, by a misleading illustration of an interesting specimen showing 5 sporophylls attached in a series, and the other from Campbells Ledge near Pittston, Pennsylvania, is so inadequately represented on *pl. 107, figs. 13 and 14*, that the originals cannot be identified from the figures. Thus it came about that *Lepidophyllum cultriforme* in America became, not the name for a species, but for a group of cogenetic species characterized by little else than oblong "sporangies with their blades still attached to them," and any one of several species may actually occur at localities from which *L. cultriforme* is listed in the literature. This name will hereafter be restricted to the species from Cannelton, of which we are refiguring the specimen originally figured by LESQUEREUX and one other from the Lacoe Collection. The "form" from Campbells Ledge becomes a new species, *C. pugiatus*; *fig. 27* is from a specimen from the Lacoe Collection.

POTONÉ (18, p. 372) figured unsatisfactorily, without description, another species from Lower Silesia, under the name *Lepidophyllum waldenbergense*, and while NATHORST was engaged upon the study of the Spitzbergen collections, he secured from the Royal Prussian Bergakademie at Berlin the type material of the Silesian species in the expectation that it might help him to interpret certain structures in *L. mirabile*. In this he was disappointed,

but he redrew the types of POTONIE and reproduced them (16, p. 64, fig. 16), remarking that an apparently non-septate sporangium, in place, with a thin plate of tissue extending for a short distance beyond it, above, might indicate an intimate relation with *Lepidocarpon* if this plate of tissue proved to be part of an investing membrane about a megasporangium. The same paper (p. 62) describes another Spitzbergen species, *L. riparium*, which is compared with *Lepidocarpon*. Although the originals of figs. 17 and 18 on pl. 13 occur in juxtaposition, we shall not hereafter include in this species the first named. In his contribution to the Carboniferous Flora of Northeastern Greenland, NATHORST (15) has appended to a series of figures of "*Lepidophyllum* cf. *lanceolatum*" two figures (34 and 35), concerning which he remarks that it is difficult to ascertain whether or not they belong to the same species as the others. It seems apparent that they do not, but instead constitute a species of *Cantheliophorus*. We shall not attempt, however, the description of a new species from these figures.

To the several species already discussed, 5 sharply characterized new species (*novaculatus*, *ensifer*, *sicatus*, *robustus*, *grandis*) are added, based upon material collected by the author from Maryland, a sixth (*subulatus*) based upon material from Kansas in the Lacoe Collection at the United States National Museum,² and a seventh (*pugiatus*), already mentioned, based upon material from the Northern Anthracite Coal Basin of Pennsylvania.

Generic characters

In this genus the sporophylls, of which the organization is somewhat complex, are borne in spiral arrangement upon an axis in the formation of a strobilus. This axis has not been observed, but the nature of the cortex is apparently such that upon the disintegration or disruption of the cone a narrow linear fragment invariably remains attached to the proximal extremity of the sporophyll pedicel. The dismemberment of the cone at maturity was apparently very complete, for in a large collection of these forms only 3 cases were observed where sporophylls are

² This is the material listed by DAVID WHITE as *Lepidostrobus cultriformis* in Bull. 211, U.S. Geol. Survey, 1903, p. 105 (excl. Lacoe Coll. nos. 16092, 16093).

attached among themselves (2 of them are figured), and curiously enough in none of these is the axis itself preserved. This sliver-like fragment of the cone axis, for facility in subsequent discussion, we shall call the "foot," that part of it which extends upward from the point of insertion shall be known as the "toe," and the downward extension the "heel." The length of the toe is usually greater than the width of the sporangiophore, but in one American species (*ensifer*) it is characteristically very long and slender, and it is a fortunate circumstance that our best series of attached sporophylls belongs to this species, for it shows conclusively that units with such length of foot must be arranged spirally to be disposed as we find them in this series.

The sporophyll pedicel is usually nearly or quite normal or perpendicular to the axis of the cone, and as a rule it is straight, although in several species (*mirabilis*, *waldenbergensis*) it regularly curves slightly upward toward the distal extremity. To the inferior, dorsal, or abaxial face of the pedicel there is attached a plate of tissue which we shall call the "keel." This structure in some species (*robustus*, *cultriformis*, *subulatus*) is relatively wide and was probably membranous or scariose, maintaining its width from the heel to which it is attached, to the distal extremity of the pedicel where it terminates abruptly. In other species (*linearifolius*, *mirabilis*, *grandis*) it is developed only distad into a sort of semispatulate structure, which was sometimes rather stout and probably ligneous from development of sclerenchyma (*linearifolius*, *grandis*). To the extremity of the pedicel is attached the lamina or blade of the sporophyll. This varies in length among the species of this genus from 1 to 12 cm. It may be narrowly and sharply triangular in shape (*cultriformis*, *ensifer*, *sicatus*), 8 mm. or less in width at base, or slender and long-linear in shape (*linearifolius*, *grandis*, *novaculatus*) and only 2-3 mm. wide at base.

The single midrib is continuous with the pedicel at the bayonet-like attachment of the blade, but at this point the blade is often flexed sharply forward, and within certain limits the angle which the blade makes with the pedicel (we shall call it the "angle of inflexion") is characteristic of a given species. In certain species (*novaculatus*, *robustus*, *waldenbergensis*) this angle is nearly or quite

90°, which means that the blades were closely appressed and the cone very slender in consequence, while in other species (*linearifolius*, *grandis*) this angle is nearly or quite 180°, which is to say that the blade is in practical alignment with the pedicel, with a result that we have a very loose bristling cone, in one species (*linearifolius*) as much as 10 inches in diameter, a striking object! In certain species, particularly those with triangular blades, the blade for nearly or quite its entire length may be folded sharply backward, lengthwise along two parallel lines where the lateral stomatiferous furrows have weakened the lamina. These two furrows upon the underside of the blade are usually separated by the space of a millimeter or less, and the angle which the lateral portions of the blade make with one another ranges from 0°, where they are parallel, to 180°, where the blade is not at all reflexed or reduplicate lengthwise. In some cases (this is particularly noticeable in *linearifolius*) these two lines share the plication unequally, one of them sometimes indeed taking all of it. In some of the species (*sicatus*, *pugiatus*) the blade is folded back only throughout the proximal half, beyond which it flattens out or becomes actually concave above. Sometimes a faint longitudinal line may be seen upon each half of the blade, roughly midway between the stomatiferous furrow and the lateral margin. In one species (*novaculatus*), in which the blade is reduplicate only at the very base, we have noted with much interest a slight torsion which is always dextrorse in passing from the base outward, this without a single exception among over 100 examples observed. At the base the blades in some species (*ensifer*, *cultriformis*, *sicatus*) are abruptly cut across, with the lateral basal angles either sharply rectangular or rounded subangular, while in other species (*novaculatus*) the lateral basal portions of the blades are prolonged downward for 1-2 mm. into auricular processes.

Borne upon the superior, ventral, or adaxial face of the pedicel, in the angle made by the pedicel and the toe, is a large platelike structure, the sporangiophore, somewhat oblong-elliptical in shape; in length only slightly in excess of that of the pedicel, bearing 2 large elongate sporangia, one upon each side of it, attached at a point well forward, a short distance above the junction of the

pedicel and the blade. The surface may be nearly plane or it may be thrown into several low longitudinal folds. It is sometimes nearly smooth (*ensifer*, *sicatus*), but it is usually granulose to the unaided eye and minutely rugulose-bullate under the lens. In some forms the units of this sculpture are isodiametric, while in other forms some of them at least are distinctly elongate transversely, and sometimes the surface is very clearly transversely rugose even to the unaided eye (*riparius*, *subulatus*). Usually there is a line, a narrow bar or a low narrow longitudinal ridge, which we shall call the "brace," dividing the face of the sporangiophore into 2 regions, which will be referred to hereafter as the "inner" or "axillary field" and the "outer field." The outermost portion of the latter, particularly when it is differentiated, will be called the "crest." In species with a great development of crest (*cultriformis*, *subulatus*) this structure extended well upward between the sporangia of the superjacent sporophylls. In a cone in which the sporophylls are arranged spirally, a given sporophyll does not regularly occur exactly beneath the interval between the two next above it, and by reason of this fact the crest of the first mentioned sporophyll is usually slightly deflected in its course into this interval, and this deflection can often still be seen upon the crests of detached examples. From a point on the toe near the middle of the narrow proximal end of the sporangiophore the brace extends forward sometimes straight toward the point of inflection, while at other times it is parallel or nearly so with the pedicel throughout much or all of its length. In the first case the axillary field has the shape of a narrow isosceles triangle, with the base along the axis of the cone; while in the second case its shape is roughly oblong-rectangular, with the distal extremity more or less acute where the brace toward this extremity is deflected toward the pedicel, which may or may not be flexed upward slightly to meet it. The outer field is sometimes oblong-rectangular, but is usually somewhat arcuate, particularly distad. The outer margin of the crest is convex. The granulations upon the face of the sporangiophore may or may not extend across the surface of the brace. These granulations sometimes extend to the outer margin of the crest (*novaculatus*), while at other times they are limited strictly to

a definite linear-oblong area above the brace and close to it (*mirabilis*).

In a plane perpendicular to that of the sporangiophore at its distal extremity is a narrow plate, as much as 2 mm. wide, which will be called the "guard," for in certain species (*linearifolius*, *grandis*) its development is such that it serves obviously for the protection of the sporangia. This guard assumes a characteristic attitude for a given species, which may be expressed in terms of the angle which it makes with the pedicel, measured in the plane of the sporangiophore. This angle ranges from practically 90° to 150°. The sporangiophore with the upper termination of the guard often forms a distinct angular or cornicular process which will be called the "beak." The brace appears to terminate against the guard usually near the junction of pedicel and blade.

The oblong or elliptical sporangia are flattened against the sporangiophore and are attached to it apparently by a relatively narrow neck. In some species they appear to have been nearly coextensive, but usually the sporangia do not extend quite to the foot nor to the outer edge of the crest. The limited space between sporophylls at the axis of the cone would allow only for greatly flattened extensions of the sporangium, and this space appears not usually to have been invaded at all. The sporangia of *cultriformis* usually did not extend within 2.5 mm. of the cone axis. Although throughout this genus normal sporangia at maturity appear generally to have become detached from the sporangiophore, the writer has found several specimens with apparently normal sporangia still in place, from which it has been possible to cut away a part and reveal the sporangiophore beneath. Several of these are figured. What may have been defective or somewhat impoverished sporangia still attached to the sporangiophore are not really uncommon. The area upon the sporangiophore once covered by a sporangium which has become detached may sometimes be known from a faint impression of the latter, and indeed the shape and size of the sporangia in some cases (*cultriformis*, *subulatus*) are as yet known only from these impressions. The surface of the sporangium, which is often traversed by a distinct median longitudinal furrow, may be smooth, farinose, or fine-granular. These sporangia

may eventually prove to be microsporangia, but until undoubted megasporangia have been discovered we prefer to consider this genus homosporous. Recognizing that practically all known paleozoic Lepidophytes are heterosporous, these must have been preceded in the phylogeny by homosporous forms.

There appears to be no evidence of a ligule, but it must be recognized that negative evidence concerning an organ as delicate as this, in the case of carbonized impressions such as these under discussion, can have very little value.

Relation of structure to environment

The distal attachment of the sporangium by a relatively narrow neck has been looked upon rather generally as archaic or primitive and subject to two obvious disadvantages (33): (1) such a restricted channel for the passage of food and water to the developing spores may lead to nutritional difficulties as the sporangia increase in size; (2) it is mechanically weak.

The first of these ideas seems to have developed largely with that theory of descent among the Lycopods which holds that *Lepidostrobus*, with the linear attachment of its sporangium, is the more highly organized and modern, and *Bothrostrobus*, with the necklike attachment of its sporangium, the more primitive, for it furnishes one plausible explanation for this modification in descent. The trabeculae and sterile plates which extend upward among the spores in the large sporangia of some of the arborescent Lycopods would add confirmation to this view if they were developed, as BOWER (5) and others believe, in response to a demand for yet greater improvement in the mechanism of nutrition. Whether or not the restricted attachment of the sporangium of *Cantheliophorus* placed it at a disadvantage in competition with other forms may for the moment be left open. That this attachment is mechanically weak is obvious, but with proper compensation in protecting structures during the period of the development of the sporangium, this very weakness, instead of a disadvantage to the plant, may become a real advantage. In this genus, owing to the weakness of this attachment, the dissemination of the sporangia with their spores must have been very thorough, for the occurrence

of a normal sporangium in place upon a detached sporophyll is rare, while, on the other hand, the sporangia of *Lepidostrobis* held so tenaciously to the sporophyll and the latter to the cone axis that both among petrifications and impressions we find long series of apparently mature sporangia in place. It is conceivable that the very mechanical excellence of this attachment might thus prove the undoing of a type in close competition with another with no such restriction upon the dissemination of its spores. This mechanical weakness in *Cantheliophorus* is well compensated for in protecting structures at the time when otherwise it might prove fatal. The most conspicuous of these is the guard and the blade. The latter protects in one of two ways. In species like *C. novaculatus* where it is flexible it is closely appressed, and in this way forms a dense, overlapping, protecting vestiture for the entire cone; while in other species, well illustrated by *C. ensifer*, it stands out formidably, rigid and sharp-pointed, like a bayonet. The simple but very efficient expedient by which this rigidity is secured is interesting from a mechanical point of view. It is secured by backward folding along the stomatiferous furrows near the midrib until the moment of inertia about the horizontal neutral axis of the cross-section approaches that about the vertical neutral axis; terms which express resistance to bending in a cantilever channel, or angle-beam of equal legs such as this. The sporangium is further protected on one side perfectly by the sporangiophore and on the other, in some species at least partially, by the crest and keel of subjacent and superjacent sporophylls respectively. Very short, lateral, flangelike wings on the pedicel serve as rests for the sporangia. The large radial sporangiophores with their tenacious hold upon both pedicel and axis, further strengthened by the brace and the guard, probably gave to the cone as a whole great stability during the period of the development of the sporangia.

In strobiloid types the increase in the volume of the sporangium by radial extension may be regarded as an efficient simple structural modification for increasing spore production, because this result may thus be accomplished without at the same time disturbing the cone by the multiplication of parts or by the modification and the increase in the size of the necessary protective structures.

Sporangia of *C. linearifolius* attain a length of 18 mm., rivaling those of *Lepidostrobus Rouvillei* Saporta and Renault, *L. Bertrandi* Zalesky, and *L. kentuckiensis* Scott, which range in extreme length to 16 or 17 mm. It would seem probable, therefore, that we are dealing with a relatively efficient type of cone.

Systematic position of genus

In the discussion of the relation of this genus to others of the Paleozoic we shall use the terminology of the systematic arrangement of the vascular cryptogams proposed in 1915 by BERRY (3, 4), and it may be prudent to give here very briefly, without annotation, the part of this classification which will concern us presently. The phylum Pteridophyta no longer embraces all the vascular cryptogams, but is restricted so as to include only the Filicales of the old scheme. The phyla Lepidophyta and Arthrophyta are established to receive the scale-leaved and the joint-stemmed vascular cryptogams respectively, thus:

PHYLUM LEPIDOPHYTA

Lycopodiales	
Lycopodiaceae	} Lycopodiales of literature (referred to in this paper as the Lycopods)
Selaginellaceae	
Lepidodendrales	
Bothrodendraceae	
Lepidodendraceae	
Sigillariaceae	
Isoetales	
Psilotales	

PHYLUM ARTHROPHYTA

Class Sphenophyllae	
Sphenophyllales	
Class Calamariae	} Equisetales of literature (excepting a few of the more recent contributions)
Equisetales	
Calamariales	
Pseudoborniales	
Protocalamariales	

In *Cantheliophorus* the sporophylls are arranged spirally upon the axis of the cone, and the slender, simple, uninervate sporophyll laminae show upon the under surface 2 lateral longitudinal grooves like the characteristic stomatiferous grooves of the usual paleozoic Lycopod leaf. Upon such evidence we must place this genus among the Lepidophyta, and we may have further evidence in

justification of this in the intimate and constant association of one species (*C. novaculatus*) with a species of "*Lepidodendron*" with small square or rhombic, closely packed bolsters, which we have suspected of being a part of the same plant. At a horizon two-thirds of a mile east of Westernport, Maryland (190 ft. below the horizon of the Davis seam), *C. novaculatus* is replaced by *C. robustus*, a very closely related species, and it may be significant in this connection that the small-bolstered species of *Lepidodendron* just mentioned is here replaced by a very similar one.

The only groups in the phylum Lepidophyta as it stands today are the Lycopods and the Psilotales. The latter constitute a small recent group of disputed position, believed by BOWER (6), THOMAS (32), and SCOTT (28) to be related more closely to the Sphenophyllales than to the Lycopods. They are characterized by lepidophytic leaf habit and furcate sporophylls supporting bilocular or trilocular synangia upon the adaxial surface. Concerning the former BOWER has said: "There is perhaps no character which marks off the plants of lycopodiinous affinity from others so clearly as the constancy of the solitary sporangium . . . it stamps this series of Pteridophytes as peculiar from all others"; to which may be added a statement from SCOTT (27): "The Lycopods constitute a wonderfully homogeneous group so neatly rounded off as to give little hold for any hypothetical link with other classes of plants."

The number and attachment of the sporangia and the position and the nature of the sporangiophore, when present, are matters of prime importance in the present classification of the vascular cryptogams, and at once the impracticability of placing *Cantheliophorus* with its conspicuous bisporangic sporangiophore among the Lycopods becomes evident. The objections to placing it among the Psilotales are almost equally insuperable, and there remains no alternative but to establish for its reception a new order, CANTHELIOPHORALES of the phylum Lepidophyta.

Phyletic relations

The question whether this group is either more or less primitive than the others of the phylum now arises for consideration. There has been a growing disposition in late years to regard the simple

relation of the Lycopod sporangium to its sporophyll as the result of reduction from more elaborate and intricate forms, but the evidence in support of this view has not been conclusive, although there appears to be very little against it. Although BOWER (7) believes that there is a preponderance of evidence in favor of amplification from simpler forms in the phyletic development of many of the Lycopods, he prefers to leave the matter "for the present open"; and Lady ISABEL BROWNE (10), after a brief impartial discussion of the question, likewise leaves it so. SCOTT (27) is inclined favorably to the alternative view, but he states: "Whether the simple relation between the sporangium and the sporophyll, which characterizes the Lycopod series, is native or acquired may be left an open question. The analogy of the Psilotales rather suggests the latter alternative, and all comparative morphology teaches how often progress consists in simplification." In 1908 Miss BENSON (2) made a very interesting contribution to this subject, in which she says: "It has been again and again suggested that we have in the lycopodinous 'sporangium' a reduced structure which is homologous with the sporangiophore of the Sphenophyllales, but the evidence in favor of this 'reduction hypothesis' is still very inadequate."

SCOTT (28) reminds us that "the ventral pad of *Spencerites* has been compared to the sporangiophore and the sterile tissue in *Mazocarpon* also by Miss BENSON," but he concludes that "these suggestions are interesting but at present too hypothetical for any conclusion as to affinity to be based on them." It is the isolation of the Lycopods that has made phyletic hypotheses concerning them so inconclusive. In spite of great structural diversity, the Psilotales do after a fashion bridge the great gap between the Lycopods and the other Paleozoic groups, but the peculiar specialization (aberrancy) of this group reduces its value for comparative purposes, and in any event, as SCOTT has said, "it is not wise to rely much on evidence from a recent family in questions of remote ancestry." A distinct new Paleozoic group showing definite affinity with the Lycopods might then well be expected to contribute to this difficult problem facts of interest and importance. "Both fusion and septation have occurred in various instances,

and in any given case the proper initial attitude is to hold that either mode of origin may have been the source of the synangial state as it now appears" (BOWER 7). Let us seek out first the facts which might appear to harmonize with the "reduction theory." If this hypothesis is the correct one for the Lepidophytes, *Cantheliophorus*, with its elaborate bisporangic sporangiophore expanded platelike in the median vertical plane of the sporophyll, would be looked upon as the representative of some primitive ancestral type, from which by reduction and simplification the Lycopods, with a solitary median sporangium resting directly upon the pedicel of the sporophyll, might have resulted. Are there any structural details in *Cantheliophorus* which are generally conceded to be primitive? The distal attachment of the sporangia is often considered to be such, but this opinion has developed so largely out of certain theories of descent, themselves resting often upon very insecure foundations, that while it should not be forgotten in summing up the evidence, it can hardly be thought of as having much weight. Assuming the correctness of this hypothesis, we might expect to find in the more reduced of several groups vestiges of structures which are functional or at least more extensively developed in ancestral forms or in the less reduced descendants of these ancestral forms. I have already quoted the suggestion by SCOTT that the ventral sporange-bearing prominence upon the pedicel of *Spencerites* may be the vestige of a sporangiophore. Miss BENSON figured and discussed at some length *Mazocarpon* from the Upper Carboniferous, with its great central core of sterile tissue and two lateral "sporogenous regions," and in the same paper also a new heterosporous form, *Lepidostrobus mazocarpon*, from the Lower Carboniferous of Burntisland, Scotland, likewise with a great central mass of sterile tissue, both in the microsporangia and megasporangia, with the sporogenous tissue arranged in an arc about it above, and she states that "it would be a very natural sequence that the sporogenous region of a single sporangiophore should become confluent, and the gradual reduction of the sterile tissue to a mere 'archesporial pad' and pedicel would next follow."

In 1872 WILLIAMSON (37) described and figured a *Lepidostrobos* (*L. Veltheimianus* Scott) in which a single continuous plate of sterile tissue usually in a median position arises from the slightly projecting subarchesporial pad and extends upward into the sporangial cavity. WILLIAMSON believed it to be "coextensive with the entire length of the sporangium," but BOWER (5) figures a section in which it does not extend quite to the distal extremity. In 1914 Mrs. AGNES ARBER (1) demonstrated the presence in *Lepidostrobos Oldhamius* Willm. of a similar plate of sterile tissue which also "died out toward the distal end of the spore sac," and the same structure was observed by this author in *L. foliaceus* Maslen, *L. Binneanus* Arber, and in an unnamed species from the Coal Measures of Great Britain discussed and figured by BOWER in 1894. BOWER also called attention to the irregular trabecular processes that "spring upwards from the floor of the sporangium (of *Lepidostrobos Brownii*) and project a considerable distance into the cavity. They are not scattered indiscriminately over the floor of the sporangium, but arise from a projecting ridge." RENAULT (21) shows similar structures in the sporangium of *L. Rouvillei* Sap. and Ren. from the south of France. Accordingly Mrs. ARBER concludes that "some form of sterile upgrowth from the sporangial floor may eventually prove to be characteristic of all forms of *Lepidostrobos* which are homosporous or microsporous, such a structure not yet having been observed in megasporangia."

The median sterile plate in the sporangium of a number of species of *Lepidostrobos* is singularly suggestive of that median plate in *Cantheliophorus* which constitutes the sporangiophore, but even should we accept their homology, and this we may not so easily escape, this fact, if considered without reference to other facts, could as well be adduced in support of one as of the other of the opposing phyletic theories of reduction and amplification. Are there any facts which might suggest to us the course of the events in the descent of these groups? Facts from ontogeny are of the utmost importance in the solution of phyletic problems, but from the very nature of fossils such facts are not usually available. We are fortunate, however, in having a few facts concerning the

immature sporangia of *Lepidostrobos*. In the immature sporangia near the apex of the cone of *L. Brownii* (Unger) Schimper, BOWER (5) has observed that "the bands of sterile tissue extend to the upper wall of the sporangium," but he has been "unable to establish beyond doubt the fact of the tissue connection between them and the wall." A section through a cone of *L. Oldhamius* Williamson, "passing obliquely through the apex and displaying the internal structure of the immature sporangia with great clearness," has been figured and discussed by Mrs. ARBER, as follows (see fig. 42):

The sterile plates in these young spore sacs are massive and well preserved and give rise with great regularity to two smaller lateral processes one on either side. The branches are not directly opposite to one another and the main process is continued above its branches for a considerable distance. That these outgrowths are of the nature of plates running in the direction of the long axis of the sporangium and are not merely peglike structures is evidenced by the fact that they present a general similarity of appearance in the seven sporangia in which they are visible in the section presented in *pl. 21, fig. 1*. Another point which is established by comparison of the different sporangia is that the sterile plate died out towards the distal end of the spore sac. In older sporangia the sterile plates are relatively less important; the lateral branch plates seem to shrivel and disappear quite early.

These very interesting facts seem susceptible of an interpretation favorable to the reduction theory, for if there is a phylogenetic recapitulation in the development of this sporangium we can scarcely escape the conclusion that at one time in the history of the race the sporangium was divided more or less completely by a stout septum into 2 loculi, and perhaps at an earlier period still into 4 loculi if we may be permitted to interpret the branches of the sterile plate of the more immature sporangia as the vestiges of a transverse sporangial septum in some ancestral form; for if we observe the relatively great size and development of this sterile plate with its branches in the least mature of this short series of sporangia, it will at once seem highly probable that in sporangia just a little less mature these branches would extend quite to the lateral wall. For the first of these hypothetical ancestral forms one could not wish for a representative more satisfactory than *Cantheliophorus*, and for the second more remote tetrasporangic

ancestor the Calamariales suggest themselves. Is there further evidence to show that the former is near such a line of descent? Unfortunately we have here no structural material which might show us stages in the development of the sporangium, but in mature sporangia of our collections the distinct median longitudinal furrow regularly encountered in several of the species may have significance in this connection, and the differentiation of the face of the sporangiophore into two more or less distinct fields might have some bearing on this matter, and it is perhaps not a mere coincidence that these fields are most sharply marked in one of the oldest known species, *C. mirabilis* from the Lower Carboniferous. While such evidence for a tetrasporangic ancestor for *Cantheliophorus* and through it for the Lycopods is exceedingly weak, it cannot be ignored.

In *Cantheliophorus* the sporangiophore is dorsiventral, while the symmetry of this structure in the most abundant of the Calamariales, *Palaeostachya* and *Calamostachys*, with a few exceptions is radial, and unless we can indicate a form somewhat intermediate between types of such essential difference, theories involving their affinity must remain inconclusive. *Calamostachys* (*Arthropitystachys*) *Grand'Euryi* Renault and *Calamostachys* (*Arthropitystachys*) *Decaisnei* RENAULT (19, 21), two species based upon petrified material from Saint-Étienne, appear to constitute such an intermediate type, for in each there is a stout plate of sterile tissue singularly like the sporangiophore of *Cantheliophorus*, which spans more or less completely the space between the sporangiophore and the bracts of the whorl above, interposing a vertical wall between sporangia borne distad upon the same sporangiophore. There is slight development also of similar tissue in this plane beneath the sporangiophore (fig. 33). Even though it be admitted that these 2 species may possibly lie near the line of descent, it may be objected that there is still a great fundamental difference between them and *Cantheliophorus*, inasmuch as the arrangement of the sporophylls is verticillate in one case, while it is spiral in the other. Such an objection, however, might easily be dismissed with a reference to *Spencerites*, a form with verticillate sporophylls, which has been placed without question in the exclusive group of the Lycopods.

Will the comparison of stem anatomy throw any favorable light upon the question of a possible remote phyletic connection between the Calamites and the Lycopods? A comparison of the stem structure of such lycopodian forms as *Sigillaria Menardi* (BRONGNIART 9) (fig. 13) with a calamitean form such as *Calamites* (*Asteromyelon*) *Augustodunense* (RENAULT 23) (fig. 14), an appendage of the stem, probably a root, of some species of *Calamites*, will at once reveal a similarity which extends to details. In both the xylem consists of a ring of somewhat wedge-shaped elements, distinct from one another but nearly or quite in contact in their wider portions except for narrow interposing medullary rays. Each xylem "wedge" consists of both primary and secondary xylem, the relatively small bundle of centripetal protoxylem occupying the apex. In each case the outer side of the protoxylem bundle is occupied by small spiral tracheids, while the remainder of the bundle, the convex inner portion, consists of larger scalariform tracheids. These primary strands are distinctly separated from one another. The secondary xylem consists of large radially arranged scalariform tracheids. Beyond the xylem is a narrow zone of phloem, and beyond this the cortex. Agreement such as this in the stem anatomy of forms from different phyla is very impressive.³ On the other hand, we can think of no lycopodian stem which even remotely suggests the characteristic triarch or hexarch protostele of the Sphenophyllales. The evidence from anatomy then gives a certain plausibility to the suggestion that *Calamostachys Grand'Euryi* Ren. and *C. Decaisnei* Ren. may represent a calamitean ancestor of *Cantheliophorus*. "True phylogenetic homologies may fairly be expected to be traced between plants which appear to belong to the same natural series" (BOWER 5), and accordingly the brace in the sporangiophore of *Cantheliophorus* and the radially symmetrical sporangiophore in *Palaeostachya* and *Calamostachys* may come to be considered

³ If by chance anyone should contend, though it is rather beside the point, that the force of this comparison is weakened somewhat by the fact that centripetal xylem, as VAN TIEGHEM first pointed out, is common to the roots of all vascular plants, we should say that the force of this comparison is correspondingly reinforced by the fact that this type of protoxylem characterizes the stem of *Protocalamites peltycurensis* (Scott) Lotsy (SCOTT 28) from the Lower Carboniferous of Scotland.

homologous. The outer field of the sporangiophore of *Cantheliophorus* might then be represented in the 2 species of *Calamostachys* just considered by the plate of sterile tissue above the sporangiophore, and the guard in one case, which is peltate with respect to the brace considered alone, would then become the homologue of the peltate extremity of the sporangiophore in the other.

The sporangiophore of *Calamostachys Decaisnei* Ren. which we have reproduced is inclined slightly toward the bracts beneath it. This may be accidental, but with just a little more inclination, together with the closing of the space between it and the bracts below by a sterile plate (of which we already see some development), we should have a sporangiophore almost precisely like that of *Cantheliophorus*. With coalescence, further, of the pair of sporangia upon each side of it and the concrescence of the 2 subjacent bracts, we should have to all outward appearances *Cantheliophorus* itself. Whether or not there are two parallel vascular bundles in the midrib of the blade of *Cantheliophorus* as possible evidence of such a history we have at this time no means of knowing, but we may recall with some interest in this connection that a species of *Sigillaria* from Autun does bear a leaf with 2 vascular bundles in the midrib, and it seems significant that in general the stem anatomy of this species closely resembles that of *S. Menardi*, which of all the known Lycopods is perhaps closest to the Calamites in this respect, as I have shown elsewhere in this paper, and according to the theory here set forth one of the most primitive. It was RENAULT (20) in 1879 who described this species under the name of *Sigillariopsis Decaisnei*.

It may be well in passing to remind our readers that according to the theory here proposed the sterile plates within the sporangia of *Lepidostrobus* were not developed, as BOWER suggested, primarily to serve for the nourishment of the spores, but it is probable that they did well serve that purpose in a sort of secondary or incidental manner, transferring nourishment to the interior of the sporogenous mass in the early stages of its development, and finally wasting as they yielded their own substance to the developing spores.

There is yet one weakness (8) in this theory of the descent of the Lycopods. "It is not enough to suggest reduction on mere

grounds of comparative convenience; to make the suggestion convincing in any group where general reduction is believed to have occurred it will be necessary to prove that the sum of nutrition, from whatever source, has diminished in the course of descent and that the reduced spore output has been the result. Until this has been shown to have occurred in any case, there seems no sufficient reason to accept as more than a quite open hypothesis any suggestion of general reduction of the sporophyte" (BOWER 7). "The hypothesis of relative primitiveness has then logically prior claim and must be accepted as a working theory until good grounds can be given for preferring that of reduction" (TANSLEY 31).

With the development of a dendritic habit among certain groups of the Lycopods came greater capacity for spore production, and this was followed up structurally in several ways, for the multiplication of spores in a homosporous plant, with equal chances of dissemination, must be considered an advantage as long as these spores can be properly matured, and in many forms it was probably not merely an advantage but a necessity to produce spores to the limit of their capacity in order to maintain themselves in the struggle for existence. Unfavorable environmental conditions, such as slow unfavorable climatic changes, may be expected to decrease the capacity for spore production, and this among plants that have been producing spores to the limit of their capacity will inevitably lead to one or more of several possible forms of reduction. There may be reduction in the number or the size of the sporangia or sterilization of some of the potential sporogenous tissue or archesporium.

During geological time there have been great periods of marine transgression, punctuated by periods of regression or continental emergence, usually accompanied by orogenic disturbances, and each of these great cycles of earth experience constitutes a geological period. Changes in the distribution and altitude of land masses toward the close of each of these periods were attended by climatic changes which were sometimes profound. They usually tended somewhat toward aridity, accompanied as a rule by a reduction of the mean annual temperature. To geologists the evidence supporting such facts is today so eminently satisfactory that they

have become almost axiomatic and may be accepted here without argument. The regular recurrence of red beds and sometimes salt and gypsum-bearing deposits toward the close of each great period conveniently marks these subperiods of continental expansion. In the Appalachian province where the Paleozoic record is unusually complete, we find the Juniata and Red Medina at or near the top of the Ordovician, the Salina toward the top of the Silurian, the Hampshire and Catskill occupying the same position in the Devonian, the Mauch Chunk in the Mississippian, and many red beds in the Permo-Pennsylvanian, the lowermost already occurring well toward the base of the Conemaugh. That periods of relative aridity and reduced temperature are in general unfavorable to plant life scarcely admits of argument, and thus during the descent of the cryptogams there have repeatedly been periods of stress during which some of them, accustomed to a certain habitat, were in all probability forced to adopt some program of reduction of the sporophyte in order to maintain themselves there. Allied forms, on the other hand, might be expected to occupy certain sheltered coastal regions where in spite of cold or general climatic aridity they could maintain themselves with little or no reductive changes, and thus it would come about upon the return of generally favorable conditions that the reduced and the primitive types might occur together. Arboreal types by reason of the specialization incident to this habit were doubtless upon the whole more sensitive to changes in the environment than the lowly herbaceous or suffrutescent forms, and it would seem very difficult to account for the *absence* of evidence of reduction among dendritic types that had survived the unfavorable periods toward the close of the Silurian, the Devonian, and the Mississippian.

Whether or not the Psilotales, the Isoetales, and the Lycopodiales (the last named, it must be remembered, are restricted in this paper to the Lycopodiaceae and the Selaginellaceae) belong to the phyletic line here proposed for the Cantheliophorales and the Lepidodendrales, is the question that now suggests itself. "When in a tissue tract the distinction between vegetative and sporogenous cells takes place late in the individual the presumption is that the distinction has been of late origin in the race. On this

basis the conclusion has been formed in certain cases that an increase in number of sporangia by septation has occurred. It is concluded that these late differentiated sterile tracts were once in the race fertile and that they were subsequently diverted from this previous condition; in fact that the ontogenetic development reflects the evolutionary history. This is exemplified in the synangia of *Tmesipteris* and the sporangia of *Isoetes*" (BOWER 7).

In the ontogenetic development of the sporangium of *Isoetes* and *Lycopodium* and the synangium of *Tmesipteris* (one of the 2 genera of the order Psilotales) there are no structures developed which might, like the sterile tissue within the immature sporangium of *Lepidostrobis Oldhamius*, suggest reduction in descent from a more intricate or elaborate form. The relation of the Isoetales to the remaining orders of the Lepidophytes is still very obscure, but is certainly closer to the Lepidodendrales than to any other, if we may judge by the radial elongation and insertion of the solitary sporangium; the trabeculae within this organ suggesting the rodlike or peglike processes within the sporangium of *Lepidostrobis Brownii*; the ligule; the secretory strands, comparable to parichnos observed in the leaves of one species; the great development of cortex, analogous to the enormous development of secondary cortical tissue, chiefly phelloderm, in the tree Lycopods of the Paleozoic; the secondary increase in the stem in which new zones of cells may have periodically taken up the cambial activities; and the dichotomous, monarch roots, like those of *Stigmaria*.

We are inclined to believe with BOWER, SCOTT, and THOMAS (32) that the furcate sporophyll with a synangium (not much unlike the group of sporangia upon the sporophyll of *Sphenophyllum majus*) resting upon its adaxial surface below the point of bifurcation in the Psilotales and the triarch stele with the xylem elements extending to the center in the smaller branches of *Psilotum* would seem to indicate that this group is related to the Sphenophyllales perhaps more closely than to any other. The stele in the stem of *Psilotum* is not much unlike that in the axis of the cone of *Cheirostrobis*, one of the Sphenophyllae from the Calcareous sandstone of Pettycur, Firth of Forth; and this, with the formation of secondary xylem at the base of the aërial stem and in adjoining parts of the rhizome

in old plants, "materially strengthens the anatomical analogy" (SCOTT 28). Concerning the relationship of the last remaining order of the Lepidophytes SCOTT states: "Recent discoveries appear to show conclusively that *Selaginella* had no direct connection with the Lepidodendrae, but sprang from a distinct and equally ancient herbaceous stock. No light has yet been thrown on the ancestry of *Lycopodium*, which certainly had no near relation to any Paleozoic forms in which the nature of the spores has been determined." The facts presented in this paper in no wise call for a revision of these conclusions. Already in the Paleozoic there were forms of heterosporous Lycopods agreeing closely with *Selaginella* of the present day, and although there has been specialization along different lines during descent, the lowly habit of the members of this group appears to have kept them so much out of competition with the more aggressive arborescent forms that there has been in all probability but little amplification or reduction throughout this great lapse of time, and together with *Lycopodium* they may perhaps be looked upon as something of a "persistent primitive type" (HUXLEY).

In 1909 Lady ISABEL BROWNE estimated the prevailing theories of Lycopodian descent as follows:

The weakest part of the theory that the Lycopod sporangium is the result of coalescence and fusion of free sporangia lies in the fact that it is among the heterosporous forms (*Lepidostrobus Mazocarpon*, *Mazocarpon*, *Isoetes*), presumably less primitive than the homosporous types, that what are regarded as the remains of a septum are most strongly developed. On the whole, the sterile tissue present in the above mentioned forms is much in excess of that found in *Spencerites*⁴ or in most species of *Lycopodium*. Similarly, on Bower's hypothesis that the sporangia of the synangia of the homosporous Psilotaceae represent the loculi of a septate sporangium, it is curious that indications of intermediate stages in the process of septation should be more marked in several heterosporous than in any homosporous members of the Lycopodiales.

The significance of these difficulties regarding the prevailing theories of Lycopodian descent becomes apparent with the proposition that the Lycopodiales, the Lepidodendrales, and the Psilotales

⁴ We are inclined to believe with WATSON (33, p. 391) that *Spencerites*, although it may have certain archaic characters, in reality is not primitive and may not even be homosporous, for as yet we have had no means of knowing that the spores are not indeed microspores.

are related among themselves more remotely even than was long supposed, for the evidence now in hand appears to indicate that upon the whole the first of these is primitive, the second reduced from possible pro-Calamarian⁵ ancestry, and the third, in the descent of which both amplification and reduction probably played minor successive rôles, specialized from pro-Sphenophyllaceous stock. The belief once prevalent that the Lycopods are related through the Psilotales to the Sphenophyllales and only remotely through the latter to the Calamariales will accordingly have to be abandoned.

Anatomical considerations

With the discovery of structural material of *Cantheliophorus* we may expect facts of great interest. If our interpretation of this form is correct, we may expect to find within the brace the fibro-vascular bundle which supplies the sporangia. In the large sporangiophores of *C. linearifolius*, at the insertion of the brace upon the toe, there are minute striae which in passing from the proximal extremity of the brace into the toe, instead of bending downward as one might expect, toward the insertion of the pedicel, bend upward, and this may perhaps be interpreted to signify that here the brace at its insertion may already have been dragged slightly downward during the evolution of the race from Calamarian or pro-Calamarian stock, somewhat after the manner of the sporangiophore of *Paleostachya vera* Seward (12), and if such is the case then we should not be surprised to find that the vascular strand makes a slight loop forward in the toe above the insertion of the brace, comparable to that in the species of *Paleostachya* just cited. It would seem further to be quite in keeping with our theory of reduction for *Cantheliophorus* to find 2 parallel vascular strands in the midrib corresponding in a way with the 2 close parallel lines sometimes seen over the median nerve upon the adaxial surface of the blade, but such suggestions in the present state of our knowledge are perhaps unduly speculative.

⁵ This is a hypothetical Calamarian ancestor, not necessarily proto-Calamarian.

Technical discussion of the species

There now follows a discussion of the species of this genus which will be technical and very brief, given in the interest primarily of stratigraphic correlation, for we believe that the members of a group with structure as intricate and diverse as this will have high stratigraphic value if treated with great systematic refinement. Details of structure already given will not as a rule be repeated here, and the discussion will be further condensed by a tabulation of the considerable number of dimensions involved.

The stratigraphy of the Pennsylvanian Period in western Maryland and adjacent parts of Pennsylvania and West Virginia has recently been studied critically by CHARLES K. SWARTZ, assisted by W. A. PRICE and the writer, among others, and a preliminary report on the results of these studies is about to be published by the Maryland Geological Survey,⁶ but reference to the "horizon of the Davis seam," to the "top of the Pottsville formation," and to the "top of the Allegheny formation" in subsequent remarks, calls for a very brief statement of final conclusions reached with regard to the limits of the Allegheny formation, inasmuch as the standard section for this region has undergone important revision. In the Georges Creek basin the Ames or Crinoidal marine fauna occupies a position about 550 ft. below the base of the Pittsburgh seam; the Brush Creek marine fauna, a position 250 ft. below the Ames; and the Davis or "Split-six" coal (the topmost unit of the Allegheny formation), 115-120 ft. below the Brush Creek.⁷ The thickness of the Conemaugh formation is thus a little over 900 ft., that of the Allegheny (upon stratigraphic and floral evidence) about 265 ft., and the Pottsville from the base of the Allegheny to the great unconformity at the top of the Mauch Chunk red shales between 200 and 250 ft.

CANTHELIOPHORUS LINEARIFOLIUS (Lesquereux).—The essential characters of this species are a very long slender blade perpendicular to the cone axis, a very large oblong sporangiophore with granulose

⁶ A fuller discussion will be presented in the "Monograph of the Carboniferous of Maryland," which will be published at a later date by the State Survey.

⁷ To the westward of the Georges Creek basin there is a gradual thinning of that part of the Conemaugh section above the Brush Creek marine horizon.

surface, and a well developed guard which is not, like that of *C. grandis*, of a length greater than the width of the sporangiophore. The brace is usually distinct.—Figs. 1, 2, 8–10.

Typical material has been collected from the roof shales of Coal B⁸ at the Boston mine, Pittston, Luzerne County, Pennsylvania, and also from a locality high on the steep eastern slope of the gorge of the Youghiogheny River, directly south of the mouth of Deep Creek, 1 mile below Swallow Falls, Garrett County, Maryland, at a horizon in the Allegheny formation (near that of the Lower Kittanning coal) 170 ft. beneath the horizon of the Davis seam.

Cantheliophorus grandis, n.sp.—This species is well characterized by a long slender blade perpendicular to the cone axis, but apparently less rigid than that of *C. linearifolium*, and by a large sporangiophore with a very long guard which is nearly perpendicular to the pedicel. It terminates in an acute, abruptly upturned beak. The somewhat rugose-undulate surface appears, with the aid of a lens, to be minutely rugulose-bullate in part. The brace is not conspicuous.—Fig. 3.

The type material has come from a shale lens beneath the massive friable conglomeratic sandstone in the rock quarry south of the county road, at Holmes, West Virginia, on the Baltimore and Ohio Railroad, 1 mile west of Corinth, at a horizon very close to the top of the Pottsville formation.

CANTHELIOPHORUS CULTRIFORMIS (Lesquereux).—The conspicuous features of this species are a large wide sporangiophore and a wide keel which with the form and attitude of the blade serve well to distinguish it. The latter curves slightly upward beyond the middle and usually opens somewhat at the same time. The surface is granulose or, like the last, minutely rugulose-bullate; the units like those of the next species are somewhat transversely elongate.—Figs. 5–7.

This species occurs in the shales of the floor of the Darlington coal at Cannelton, Beaver County, Pennsylvania, correlated by WHITE (36) with the Upper Kittanning.

Cantheliophorus subulatus, n.sp.—This species is sharply defined by the expansive development of the sporangiophore and

⁸ The more important coal seams in the anthracite field of Pennsylvania beginning at the base of the Lower Productive Measures (Allegheny formation) have been listed alphabetically in certain State Geological Survey publications. Coal B is supposed to be the equivalent of the Lower Kittanning of western Pennsylvania.

the keel, and by the straight, relatively short, slender blade projecting from the extremity of the pedicel without appreciable flexure, the lateral portions folded sharply back for practically their entire length. The surface of the sporangiophore is rugose with minute, close, irregular transverse folds which vary much in distinctness in different specimens.—Figs. 11 and 12.

The species occurs in the Cherokee shales (Kittanning group of the Allegheny formation) at the Penitentiary shaft, Lansing, Kansas, and in the floor shales of the Darlington coal (Upper Kittanning) at Cannelton, Pennsylvania (Lacoe collection no. 16100 U.S. Nat. Mus.).

***Cantheliophorus ensifer*, n.sp.**—The salient features of this species are great length of toe (which distinguishes it at once from all others known to us at this time), a straight, rigid, narrowly triangular blade which makes a wide angle with the pedicel, and the smooth surface of the sporangiophore, which is usually thrown into several rather prominent longitudinal folds. The guard extends forward in a position directly above and usually in contact with the superior surface of the blade.—Figs. 15 and 16.

It is abundant at a horizon 1.25 miles below Swallow Falls, Garrett County, Maryland, along the old lumber tram on the steep eastern slope of the Youghiogheny River gorge, not far below the mouth of Deep Creek, about 400 ft. below the horizon of the Davis seam (the top of the Allegheny), and 130 ft. below the top of the Pottsville formation.

***Cantheliophorus novaculatus*, n.sp.**—The noteworthy features of this species are the linear blade reduplicate only near the base, flexed forward into a position nearly parallel to that of the axis of the cone, and the sporangiophore with a fine granulose surface and a distinct brace. The keel was never wide, and it appears to have been rather frail, for often it is missing entirely.—Figs. 29 and 30.

This species is one of rather wide distribution in the Maryland area, and up to this time has been found only within the Allegheny formation. It has been collected by the writer near Warnocks Station, West Virginia, along the Western Maryland Railway, 25 ft. below the horizon of the Davis seam (top of the Allegheny); at Barrelville and Sunnyside from the roof shales of the Parker Coal, 50 ft. below horizon of Davis seam; south of Franklin, West Virginia, along the Western Maryland Railway, 75 ft. below the Davis; on the north fork of Jennings Run, northwest of Wellersburg, Pennsylvania, 95 ft. below the Davis; along foot path up the cliff above the Western Maryland

Railway west of Westernport, Maryland, 115 ft. below the Davis; along the Western Maryland Railway opposite Dodson, Maryland, 165 ft. below the Davis and along the Baltimore and Ohio Railroad; opposite Luke, Maryland, at the base of the Allegheny, 265 ft. below the horizon of the Davis. In the southern anthracite field of eastern Pennsylvania it has been collected at several localities from the roof shales of the Buck Mountain, or Twin Coal, 3 miles south of Tremont, Schuylkill County, Pennsylvania, in the Sharp Mountain Gap of Swatara Creek.⁹

Cantheliophorus robustus, n.sp.—This species is very similar to *C. novaculatus* in general appearance, but may be distinguished by greater relative width of the sporangiophore and of the keel, while the surface of the sporangiophore is smooth or farinose and not granulose. It is usually slightly larger throughout, but there is considerable range in size within a single collection.—Figs. 25 and 26.

The species occurs abundantly 1 mile east of Westernport at a horizon 190 ft. below that of the Davis seam.

Cantheliophorus sicatus, n.sp.—Among the more noteworthy features of this species is the smooth sporangiophore with surface usually thrown into several longitudinal folds. The blade is short, as a rule not much over 12 mm. in length, and makes an angle with the pedicel customarily of 150–180°, but the range must be given as 120–180°. It is narrowly triangular, usually sharply reduplicate and straight, but is sometimes curved well upward and may be open (nearly flattened) for most of its length.—Fig. 28.

In Maryland we made two large collections of this species from the Allegheny formation, one of them 1.5 miles east of Stoyer along the Western Maryland Railway associated with *C. linearifolius* (which see), 1 mile below Swallow Falls on east bluff of the gorge of the Youghiogheny River, Garrett County, 170 ft. below the horizon of the Davis seam. It occurs somewhat sparingly in the lowermost Allegheny, one-eighth of a mile east of Piedmont, West Virginia, in shales above the upper seam of coal exposed along the Baltimore and Ohio Railroad tracks, 260 ft. beneath the horizon of the Davis seam, and also in the shales above the Lower Coal exposed a short distance to the eastward of the last along the Baltimore and Ohio Railroad at a horizon 270 ft. beneath that of the Davis seam (possibly in the uppermost Pottsville). There is some question as to the precise systematic position of 2 imperfect specimens of *Cantheliophorus* very close to *C. sicatus* from a horizon east of Bond along the

⁹ Listed as *Lepidophyllum cultriforme* by DAVID WHITE, 20th Ann. Rept. U.S. Geol. Survey, 1900, p. 825.

Baltimore and Ohio Railroad, 430 ft. beneath that of the Davis seam (165 ft. plus or minus beneath the top of the Pottsville), and while it is not prudent to extend the range of this species upon the testimony of questionable material, I shall make a record here awaiting further collection.

Cantheliophorus pugiatus, n.sp.—This species is not far different from the last, but as a rule it is larger, with a blade usually more than 15 mm. in length, making an angle with the pedicel ranging from 100° to 150° , but generally falling between 110° and 140° . The keel is wider. We have figured a typical specimen of each of these related species which will usually serve well to distinguish them, but we must caution that certain small atypic forms of this species might be confused with the last.—Fig. 27.

The type material in the Lacoe Collection at the United States National Museum has come from the Pottsville formation at Campbells Ledge near Pittston, Luzerne County, Pennsylvania.

CANTHELIOPHORUS WALDENBERGENSIS (Potonié).—This species has the general habit of *C. novaculatus* and *C. robustus*, but the keel is distinctly different, showing great expansion from the heel, where it is very narrow, to the distal extremity of the pedicel, where it terminates rather abruptly.—Figs. 19–21.

The type material has come from the Waldenberg series, equivalent in general to our Lower Pottsville from Segen-Gottes-Tiefbau near Altwasser, Lower Silesia.

CANTHELIOPHORUS RIPARIUS (Nathorst).—This species may be compared with *C. subulatus*, but the beak is more prominent, the sporangiophore relatively longer, and the keel narrower. The sculpture on the surface of the sporangiophore of this species, however, will alone serve to distinguish it.—Fig. 4.

The type was collected by *Norberg* in 1913 from the Lower Carboniferous at Örretelven, Spitzbergen.

CANTHELIOPHORUS MIRABILIS (Nathorst).—This species has the habit somewhat of *C. linearifolius* and *C. grandis*, but the resemblance to these species is not close. One of the most distinctive features is the sharp differentiation of the fields of the sporangiophore.—Figs. 22–24.

The material upon which the species has been based was collected in 1913 by the Hoel-Straxrud Expedition from the Lower Carboniferous or Culm at

TABLE 1*

Canthelophorus	Diameter of cone	Length of sporangiothore	Width of sporangiothore	Length of blade	Width of blade at base	Inflexion, blade to pedicel	Length of pedicel	Length of toe	Length of heel	Width of keel near point of inflexion	Length of guard	Inclination, guard to pedicel	Length of sporangium	Width of sporangium	Formation
1. linearifolius (Lx.)	250 ±	18-20	6-9	100 ±	2-3	135-160°	17-18	5-6	1-2	0-0.5	2-3	5	120-130°	4-6	Middle Allegheny (Kittanning Group), Pa., Md., Uppermost Pottsville, W. Va., near Md.
2. grandis, n.sp.	200 ±	15 ±	9-12	90 ±	2	160-180°	11-12	6-7	1-2	0-0.5	2-2.5	10	100-110°	?	?
3. cultriformis (Lx.)	75 ±	15	7-10	20-30	3-4	150°	13-15	7	3	3	3-4	120°	10	5	Middle Allegheny (Kittanning Group), Pa.
4. subulatus, n.sp. ...	90 ±	14-17	12 ±	20-25	3	180° ±	12-16	3-6	3-5	4-6	4 ±	120°	10	5	Middle Allegheny (Kittanning Group), Pa.
5. ensifer, n.sp.	60-70	8-11	6-8	14-26	5-8	135-180°	6-8	10-14	2-4	1.5	3-4	120-130°	8	4	Upper Pottsville, Md.
6. sicatus, n.sp.	30-40	5-7	2.5-3	9-15	4	120-180°	6	2	1-2	1	2-2.5	120-140°	5-7	1.5-3	Middle Allegheny to uppermost Pottsville, Pa., Md., W. Va.
7. pugiatus, n.sp.	30-50	6-10	3-4	15-25	4-5	100-150°	6-8	2-2.5	2-2.5	1-1.5	2-4	120° ±	7	3	Upper Pottsville, Campbells Ledge, Pittsburg, Pa.
8. novaculatus, n.sp. .	20-30	7-8	3-4.5	15-40†	1.5-2	90-100°	5-7	2.5-4.5	1-2	0.5-1.5	0.5-1.5	100-120°	5-7	3-4	Throughout Allegheny formation, Pa., Md., W. Va.
9. robustus, n.sp.	20-30	6-10	4-6	20-25	2 ±	90-120°	6-9	3-5	2-3	2-3	2.5-3	90-100°	5-7.5	3-4.5	Middle Allegheny (Kittanning Group), Md.
10. waldenbergensis (Potonié).....	20-35	8-9	5 ±	20-30	?	110-130°	6-8	4-5	2	0.5-1.5	2-3	120-130°	6	3	Waldenberg series (Lower Pottsville), Silesia
11. riparius (Nath.)..	70-80	16	8-9	20	?	180°	13 ±	4 ±	2.5 ±	2.5	5	125-130°	10-11	5-5.5	Lower Carboniferous (Pocono), Spitzbergen
12. mirabilis (Nath.)..	70 +	8-10	3-4	25-35	1.5-2.5	150-165°	7 +	2 +	2 ±	0.5	0.5-1.5	140-150°	?	?	Lower Carboniferous (Pocono), Spitzbergen

* All dimensions in mm.

† Infrequently as much as 60 mm.

Camp Miller, Spitzbergen, from beds which have been correlated with the Calcareous sandstone series of Scotland and the Pocono of the Appalachian Province.

Cantheliophorus has a wide geological range which, like the ranges of the several species, may be extended as the result of careful systematic study of other collections, the stratigraphic position of which is known with precision, and it is to be expected that the limits of the normal ranges of some of these dimensions will be somewhat extended, while all of them are likely to be crossed occasionally in the case of supernormal or subnormal individuals.

The genus appears from the evidence in hand to have become extinct about the close of the Allegheny as the result of certain conditions which were unfavorable to arboreal types, for the tree Lycopods were very greatly restricted at this time. The first red beds of the continental period of the Permo-Pennsylvanian appear in Maryland less than 100 ft. above the highest occurrence of *Cantheliophorus*.

Concerning new specific names

In conclusion we feel that we should urge that greater care be exercised in the selection of new specific and even generic names by the paleobotanists who are devoting themselves to the study of structural material. MASLEN (14) in 1899 proposed the specific name *foliaceous* for an unnamed species of *Lepidostrobus* figured earlier by WILLIAMSON (38), overlooking the fact that LESQUEREUX (13) in 1880 had already used this combination. The specific name *Veltheimianus* proposed by SCOTT for a petrified cone of *Lepidostrobus* from the Calcareous sandstone of Scotland, also figured by WILLIAMSON, was employed in the same connection in 1873 by FEISTMANTEL (11) for the impression of an entirely different cone from the Lower Carboniferous of Rothwaltersdorf, Silesia. The name *Lepidostrobus gracilis*, proposed in 1914 by Mrs. AGNES ARBER for a petrified cone from the Lower Coal Measures of Great Britain, was employed in 1853 by NEWBERRY (17) for a cone from Cuyahoga Falls, Ohio, and again in 1877 by SCHMALHAUSEN (25) for a different cone from the Ursa Stufa of Ogur, Siberia. SCOTT and JEFFREY (30) in 1914 published a description of a petrified

cone from the Chattanooga shales of the Waverly Group (Lowermost Mississippian) west of Junction City, Boyle County, Kentucky, which they named *Lepidostrobus Fischeri*, but for this SCOTT has since proposed instead the name *L. kentuckiensis* (29) after ZEILLER had called his attention to the fact that RENAULT (22) had used this combination in 1890 for an impression from the Commeny Basin of France.

Another case to which attention should be called has to do with the use of the term *Lepidocarpon* by SCOTT (26) for the well known seed-bearing strobilus from the Coal Measures of Great Britain, for this name in the form of *Lepidocarpus*, which by the generally accepted rules of nomenclature must be regarded as the same term, has already been employed first by ADANSON in 1763 for a genus of African Proteaceae now included in the genus *Scolymocephalus*; by WEINMANN in 1747 and again by KORTHALS in 1855 for a genus of tropical Rosaceae included now in the genus *Ferolia* Barrère (1741). It is with much hesitation that I disturb a term of such standing as *Lepidocarpon*, and except for yet another case of the prior use of this term generically I should not have done it, for such procedure is certain to cause annoyance and sometimes irritation as well. I refer to the use of the term *Lepidocarpus* by ROTHPLETZ (24) in 1880 for the sporangia of *Lepidodendra* from the Culm of Saxony, so closely comparable to the use made of it by SCOTT that we believe that it should not have been used in its present form in the sense proposed by the latter.

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EXPLANATION OF PLATES IX-XI

PLATE IX

FIG. 1.—*Cantheliophorus linearifolius* (Lesq.); Allegheny Formation, Pittston, Pa. (type in Lacoe Coll. U.S.N.M. no. 16069).

FIG. 2.—Same; $\times 2$.

FIG. 3.—*C. grandis*, n.sp.; Pottsville Formation, Holmes, W.Va. (collection Md. Geol. Survey).

FIG. 4.—*C. riparius* (Nath.); Lower Carboniferous, Spitzbergen (Nathorst: Nachtr. Pal. Flora Spitzbergens 1914. *pl.* 13. *fig.* 18).

FIG. 5.—*C. cultriformis* (Lesq.); Allegheny Formation, Cannelton, Pa. (type, Lacoe Coll. U.S.N.M. no. 16087) (Lesq. Coal Flora. III. 1884. *pl.* 108. *fig.* 2).

FIG. 6.—Same; $\times 2$.

FIG. 7.—Another specimen from same locality (U.S.N.M. no. 16088).

FIGS. 8-10.—*C. linearifolius* (Lesq.); Allegheny Formation, Swallow Falls, Md.; fig. 9 with a part of sporangium in place (Coll. Md. Geol. Survey).

FIGS. 11, 12.—*C. subulatus*, n.sp.; Allegheny Formation, Lansing, Kansas (Lacoe Coll. U.S.N.M. nos. 16095, 16096).

PLATE X

FIG. 13.—Section of stem of *Sigillaria menardi* Brongt. much enlarged (Brongniart: Archives d'Hist. Nat. 1:1839. pl. 25. fig. 4).

FIG. 14.—*Calamites* (*Asteromyelon*) *Augustodunense* Renault (Renault: Autun et Epinac. 1893. pl. 56. fig. 6).

FIGS. 15, 16.—*Cantheliophorus ensifer*, n.sp.; Pottsville Formation, Swallow Falls, Md. (Coll. Md. Geol. Survey).

FIGS. 17, 18.—*Cantheliophorus* sp.; Lower Carboniferous, Greenland (Nathorst: Groenlands Nord-oestkyst 1911. pl. 16. figs. 34, 35).

FIGS. 19-21.—*C. Waldenbergensis* (Potonié); Waldenberg Series, Silesia (Nath. Nachtr. Pal. Fl. Spitzbergen 1914. fig. 16, p. 64).

FIGS. 22-24.—*Cl. mirabilis* (Nath.); Lower Carboniferous Spitzbergen (Nath. 1914, loc. cit. pl. 13, figs. 30, 28, 26); $\times 2$.

FIGS. 25, 26.—*C. robustus*, n.sp.; Allegheny Formation, Westernport, Md.; part of sporangium in place on fig. 25. ($\times 2$) (Coll. Md. Geol. Survey).

FIG. 27.—*C. pugiatus*, n.sp.; Pottsville Formation, Campbells Ledge, Pittston, Pa. (Lacoe Coll. U.S.N.M. no. 16108).

FIG. 28.—*C. sicatus*, n.sp.; Allegheny Formation, above Schell, W.Va. (Coll. Md. Geol. Survey).

FIGS. 29, 30.—*C. novaculatus*, n.sp.; Allegheny Formation, Franklin, W.Va.; fig. 29 with attached sporangium partly cut away to expose the sporangiophore beneath; both figs. $\times 2$ (Coll. Md. Geol. Survey).

FIG. 31.—Same species. Allegheny Formation, Luke, Md. (Coll. Md. Geol. Survey).

FIG. 32.—*Lepidodendron* sp. (to be described later); Allegheny Formation, Barrelville, Md.; suspected of being the impression of the stem of the tree which bore *C. novaculatus*.

FIG. 33.—*Calamostachys Decaisnei* Renault (Rech. sur Végét. Silicifiés. Mem. Soc. Eduenne 1878. pl. 4. fig. 12).

PLATE XI

FIG. 34.—Diagrammatic sketch of *Cantheliophorus*: *a*, toe; *b*, heel; *c*, keel; *d*, sporophyll pedicel; *e*, blade; *f*, inner or axillary field; *g*, outer field; *h*, brace; *i*, crest; *k*, guard; *l*, beak; *m*, angle of inflexion, blade to pedicel; *n*, angle of inclination, guard to pedicel; *o*, sporangium; *p*, point of inflexion; *q*, wing of pedicel.

FIG. 35.—Same, seen from above.

FIG. 36.—Diagrammatic cross-section (tangential) through sporangia borne by single sporangiophore of *Calamostachys Decaisnei* Renault, showing relation of sterile tissue (black) to sporogenous tissue.

FIG. 37.—Similar section for *Cantheliophorus*.

FIG. 38.—Same for *Lepidostrobus*.

FIG. 39.—*Lepidostrobus Mazocarpon*, after Miss BENSON; microsporangium in cross-section, $\times 15$ (New Phytol. 7: 1908. fig. 26, p. 145).

FIG. 40.—*Mazocarpon*, after Miss BENSON, $\times 15$. (loc. cit. 1908. fig. 25, p. 144).

FIG. 41.—*Lepidostrobus Veltheimianus* Scott, after WILLIAMSON (Phil. Trans. Roy. Soc. Lond. 1872. pl. 44, fig. 25); $\times 22$.

FIG. 42.—*Lepidostrobus Oldhamius* Williamson, after Mrs. AGNES ARBER (Trans. Linn. Soc. Bot. II. 8: pl. 21. fig. 1. 1914); $\times 7$; section obliquely through apex of cone illustrating the sterile tissue within the immature sporangia.